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Effects of compressive non linearity on insect based motion detection

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ABSTRACT

Motion detection and velocity estimation systems based on the study of insects tries to emulate the extraordinary visual system of insects with the aim of coming up with low power, computationally simple, highly efficient and robust devices. The Reichardt correlator model is one of the earliest and the most prominent models of motion detection based on insect vision. In this paper we try to extend the Reichardt correlator model to include an additional non-linearity which has been seen to be present in the fly visual system and we study its effect on the contrast dependance of the response and also try to understand its influence on pattern noise. Experiments are carried out by adding this compressive non-linearity at different positions in the model as has been postulated by previous works and comparison of the physiological data with modelling results is done.

Keywords: Reichardt correlator, pattern noise, contrast saturation, artificial insect vision.

1. INTRODUCTION

Insects despite their tiny brain, can easily outperform most current man-made autonomous vehicles in many ways. This can be clearly seen from the chasing behaviors of the male flies and from the ability of bees to assess distance travelled in a novel environment on the basis of visual motion cues. Such extraordinary capabilities of insects could be due to the ability of their visual system in the adaptation of visual information processing to the specific requirements of behavioural tasks and to the specific spatio-temporal properties of the natural input and the extraordinary speed with which they process retinal images.

Of the various models of motion detection based on insect vision, the earliest and the most prominent model is the Reichardt correlator model which was developed by Hassenstein and Reichardt in 1956.[1] The Reichardt correlation motion detector possess a highly parallel architecture. Each elementary motion detector (EMD) detects motion in a preferred direction by comparing a signal from one receptor with a delayed signal from an adjacent receptor. The comparison is performed using a nonlinear, multiplicative interaction between the two channels. Two EMDs tuned to opposite directions are combined to form a bidirectional motion detector.

Most of the spatiotemporal energy models, the dominant models for motion detection in vertebrates, are mathematically equivalent to correlator models.[2] Correlator models have been applied to explain motion

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detection in humans, birds and cats.[3–5] Though insects and humans are capable of estimating image velocities,[6,7] the basic correlator model does not function as a velocity estimator. It reliably indicates directional motion of sinusoidal gratings, but the response depends on contrast (brightness) and spatial frequency (shape) as well as velocity.[8] Analysis and simulations suggest that the processes commonly found in visual systems, such as pre-filtering, response compression, integration, and adaptation, improve the reliability of velocity estimation and expand the range of velocities coded.[9–15]

The stimulus that we give to our elaborated EMD model[16] is a natural image. Natural image statistics are highly predictable and biological systems are optimised to take advantage of these statistics. Differences in the local structure of various natural images result in variations in the correlated response of local detectors, which we call 'pattern noise'. We investigate this pattern noise through both electrophysiology in our model insect animal *Eristalis tenax* and with our elaborated Reichardt model.[16,17] It is found from our experiments that addition of a static compressive non-linearity, saturation has a profound effect on the shape of the pattern noise. Hence we further investigate pattern noise on the response of our model by implementing saturation at different positions of the model.

Earlier work on contrast saturation has shown that it can help in decreasing the dependance of the correlator response to contrast, thereby enabling more reliable velocity estimation.[18] So here we have also tested the effect of saturation in the contrast response of our model by implementing saturation at different positions in our model and testing it at different contrasts.

2. PATTERN NOISE

Differences in the structure of scenes result in variations in the correlator response termed as the pattern noise. The pattern noise here is not a random source of noise. It is most likely due to excitation of individual local motion detectors. Arrays of such detectors could provide spatially distributed information which is integrated at or before the level of wide field motion sensitive cells such as HS. Spatial pooling from just a single pair of HS cells might be enough to smooth out the pattern noise.[16]

Physiological motion detectors suffer from random noise, which is due to the variation in its response on repeated presentation of identical stimulus patterns. The random noise experienced by a biological motion detector falls into two categories namely photon noise and intrinsic noise. The photon noise results from variations in the number of photons absorbed by a photoreceptor in a given unit of time. In addition, the neurons and synapses that comprise the correlator generate intrinsic noise. Studies done on the LMCs (Lamina Monopolar Cells) by Laughlin[10] indicates that photon noise dominates intrinsic noise up to moderate light intensities and at higher light intensities, photon noise equals intrinsic noise in magnitude.

Dror conducted studies on photon noise using natural images and found that while photon noise leads to a slight increase in relative error, its contribution is small compared to that of pattern noise suggesting that the performance of a velocity estimation system based on Reichardt correlators depends primarily on responses to pattern noise.[18]

2.1. Pattern noise at different contrasts and different speeds

In order to understand the effect of pattern noise at different speeds and at different contrasts, we have done physiological and modelling experiments[16,17] using the same image shown in Figure 1 , at high and low contrasts at speed 180 degrees per second, which is close to the optimum velocity in *Eristalis tenax* and at a higher speed of 720 degrees per second.

2.2. Electrophysiological results

We have done electrophysiology experiments[17] at the speeds 180 degrees per second and 720 degrees per second both at high (contrast of 1) and low contrasts (contrast of 0.2). This gives us an understanding on how pattern noise is affected at different contrasts and at different speeds. Figure 2 and Figure 3 shows the response of a HS neuron at two different speed and at two different contrasts. And it is seen that pattern noise is less significant

Fig. 1. The panoramic natural image given as stimulus to the EMD model. A panorama of the image is formed by 'warping' 12 image tiles at 30° intervals to remove lens distortions and then by wrapping its ends together using Apple Quicktime VR software on a Macintosh computer.

at low contrasts and low speeds as expected. It is also clear from Figure 2 and Figure 3 that the shape of the pattern noise is also affected at different contrast which makes us wonder if there are more factors which could be affecting pattern noise and this has lead us to investigate further on whether saturation (compressive nonlinearity) which is proved to be present in the fly visual system could have a role in influencing pattern noise. So in our model we tested the results with saturation which is shown in the next subsection.

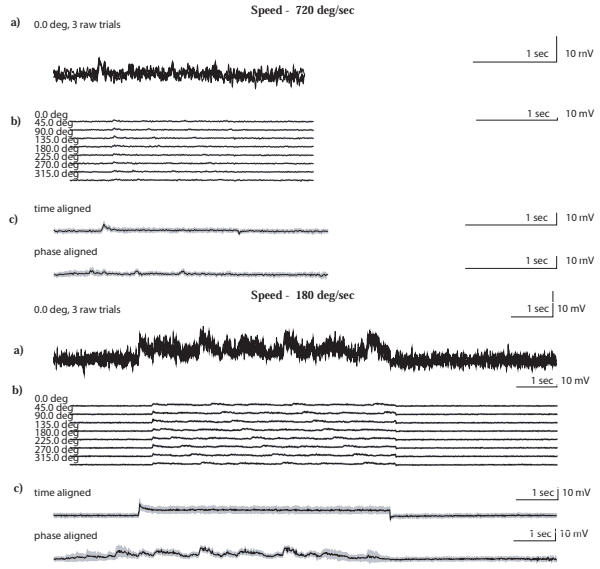


Figure 2. This figure shows the effect of 'pattern noise' on response of a single fly wide-field motion detecting neuron (HS cell) to a natural image (see Figure 1), with the image presented moving at high speed of 720 degrees per second and low speed of 180 degrees per second at 8 different initial phases, each 45 degrees apart at a very low contrast of 0.2. For each combination of velocity and image, part (a) shows three responses to identical experimental conditions. Part (b) shows the mean of at least three responses at each of several stimulus positions. Part (c) show the mean response in black and the standard deviation of the response around the mean in gray. The responses were 'phase aligned' by compensating for the position change before averaging. The 'time aligned' response shows the individual responses at each initial position averaged without compensating for position change.[17] Inspection of the individual responses and the phase aligned response indicates that pattern noise is less significant at low speeds and at low contrasts.

2.3. Modelling results

In order to understand the variation of pattern noise at different contrasts and speeds, modelling experiments were done using our elaborated EMD model[16] at the speeds 180 degrees per second and 720 degrees per second both at high (contrast of 1) and low contrasts (contrast of 0.2) with the same image as used for previous experiment. We have compared the model without saturation to the model which has output saturation

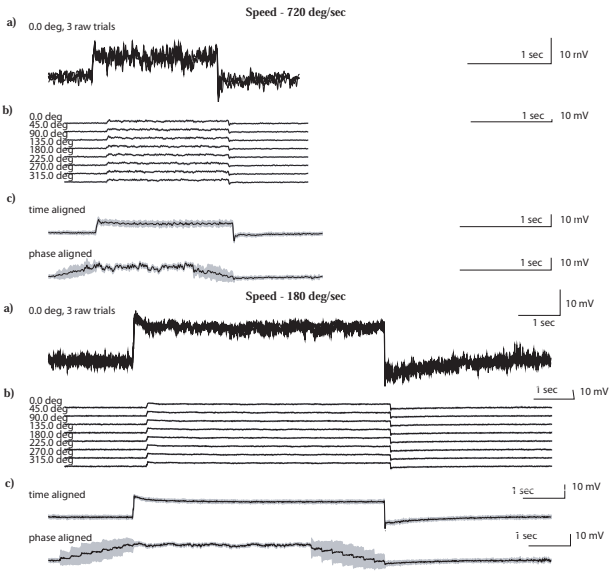


Figure 3. This figure shows the effect of 'pattern noise' on response of a single fly wide-field motion detecting neuron (HS cell) to a natural image (see Figure 1), with the image presented moving at high speed of 720 degrees per second and low speed of 180 degrees per second at 8 different initial phases, each 45 degrees apart at a high contrast of 1. For each combination of velocity and image, part (a) shows three responses to identical experimental conditions. Part (b) shows the mean of at least three responses at each of several stimulus positions. Part (c) show the mean response in black and the standard deviation of the response around the mean in gray. The responses were 'phase aligned' by compensating for the position change before averaging. The 'time aligned' response shows the individual responses at each initial position averaged without compensating for position change.[17] Inspection of the individual responses and phase aligned responses indicates that pattern noise is prominent at higher contrasts and higher speeds than at lower contrasts and low speeds.

(saturation implemented on the mean correlator response) to investigate the effect of saturation on pattern noise. Figures 4,5,6 and 7 shows the simulated response of the model with and without saturation. It is seen that like the physiological results, modelling results also show that pattern noise is less significant at low speeds and at low contrasts. Comparison of the model with saturation and without saturation shows that saturation, implemented at the output affects the pattern noise at high contrast by reducing the magnitude of the response and changing the shape of the pattern noise, as can be seen from the phase aligned response in Figure 6 and Figure 7. And clearly from Figure 4 and Figure 5, we can see that saturation has no effect whatsoever at low contrasts, as expected, with the saturated and unsaturated results being the same at low contrasts, as the response saturates only at higher contrasts. The differences that can be seen in the modelling and physiological results could be because saturation may be present at other points other than the output stage or more than one point in the fly motion pathway.

3. EFFECT OF A COMPRESSIVE NONLINEARITY (SATURATION) ON PATTERN NOISE

Both simple and elaborated Reichardt correlators show an increase of response amplitude with stimulus contrast. The neural and behavioral responses of the fly display such a dependence only at very low contrasts. As contrast increases above a few percent, the response begins to level off due to a static, compressive nonlinearity which is termed as contrast saturation.[18] This is due to limitations in the range of responses that can be signaled by physiological mechanisms.

In order to understand the effect of saturation on pattern noise, we have tested our elaborated Reichardt

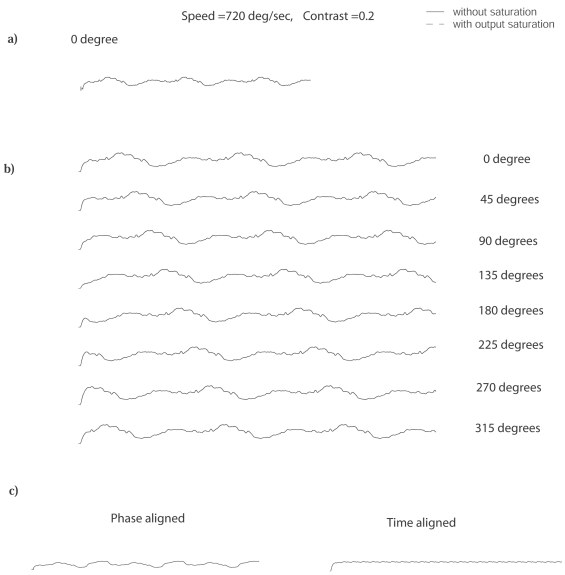


Figure 4. This figure shows the simulation results obtained by running the model with and without implementing output saturation, at 720 degrees per sec at a low contrast of 0.2 using the same image, at 8 different initial phases, each 45 degrees apart, as done in the physiological experiment shown in Figure 2. Part (a) of the graph shows the response with and without saturation at phase zero. Part (b) shows the response with and without saturation, to each of the 8 configurations. Part (c) shows the response with and without saturation, averaged in two ways, time aligned and phase aligned.[17] Like the physiological result shown in Figure 9, the modelling results also show that the pattern noise is less significant at low contrasts. Comparison of the results obtained with and without adding saturation shows, that addition of saturation has no effect at low contrasts as expected, as the response saturates only at higher contrasts.

model[16] by incorporating saturation at different positions on the model and we found that addition of saturation at different points result in changing the shape of the pattern noise. When we compare the biological results with the modelling results it is seen that there is some kind of compressive non-linearity present in the system, which causes changes in the pattern noise. So saturation was implemented at three positions in our model. One is at the photoreceptor output, that is after the spatial filtering and the next it was implemented at the correlator arms at the multiplication stage and finally we also tried implementing it at the output on the mean of the correlator output. The modelling results for the each of this case and with different combinations of them at high and low contrasts is given here.

3.1. Saturation at the correlator input

Saturation of the visual signal first occurs in the photoreceptors, which respond roughly to logarithm of luminance.[10] Saturation reduces relative error partly by reducing contrast difference from one region of the image to another. It is seen in flies that this saturation occurs primarily after linear pre-filtering but before the multiplication operation indicating that contrast saturation must take place after elimination of the mean light intensity from the signal.[8,18] Saturation is modelled here by including a compressive non-linearity such as a hyperbolic tangent function of the form, $\rho(C) = \tanh(C)$.

Figure 8 shows the phase aligned simulation results obtained by running the model at 180 degrees per sec using the same image, at 8 different initial phases, each 45 degrees apart. As we have done before, in the phase aligned method, we align each phase delayed response by shifting each response along the x-axis with the data obtained for phase zero and then we average it. The pattern noise present is clearly seen. In this case we have implemented saturation at the correlator input after the spatial filtering stage.

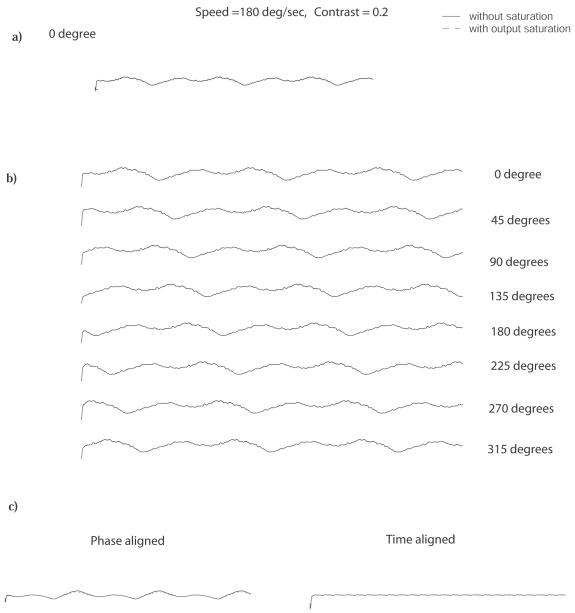


Figure 5. This figure shows the simulation results obtained by running the model with and without implementing output saturation, at 180 degrees per sec at a low contrast of 0.2 using the same image, at 8 different initial phases, each 45 degrees apart, as done in the physiological experiment shown in Figure 2. Part (a) of the graph shows the response with and without saturation at phase zero. Part (b) shows the response with and without saturation, to each of the 8 configurations. Part (c) shows the response with and without saturation, averaged in two ways, time aligned and phase aligned.[17] Like the physiological result shown in Figure 9, the modelling results also show that the pattern noise is less significant at low contrasts and low speeds. Comparison of the results obtained with and without adding saturation shows, that addition of saturation has no effect at low contrasts as expected, as the response saturates only at higher contrasts.

3.2. Saturation at the correlator arms

It is seen that saturation also takes place on both the delayed and undelayed arms of the correlator with saturation on the delayed arm following the delay filter.[8, 18] So based on this, we have implemented compressive nonlinearity before the multiplication operation on both correlator arms.

Figure 9 shows the response of the phase aligned simulation results obtained by running the model at 180 degrees per sec using the same image, at 8 different initial phases, each 45 degrees apart. In this case we have implemented saturation at the correlator arms at the multiplication stage. It is seen that the shape of the pattern noise is different from the previous case where we had implemented saturation at only the input stage.

3.3. Saturation at the output

The outputs of the wide field neurons are also found to saturate due to shunting of the membrane potential.[12] This is introduced as a compressive non-linearity following spatial integration.[18] Such an effect will flatten the peaks of the velocity response curves effectively allowing neuron to use more of its dynamic range to signal low velocities. So based on this we have implemented saturation at the output stage of our model.

Figure 10 shows the response of the phase aligned simulation results obtained by running the model at 180 degrees per sec using the same image, at 8 different initial phases, each 45 degrees apart. In this case we have implemented saturation at the output stage on the average EMD response. Note that the shape of the pattern noise is different from the previous two cases.

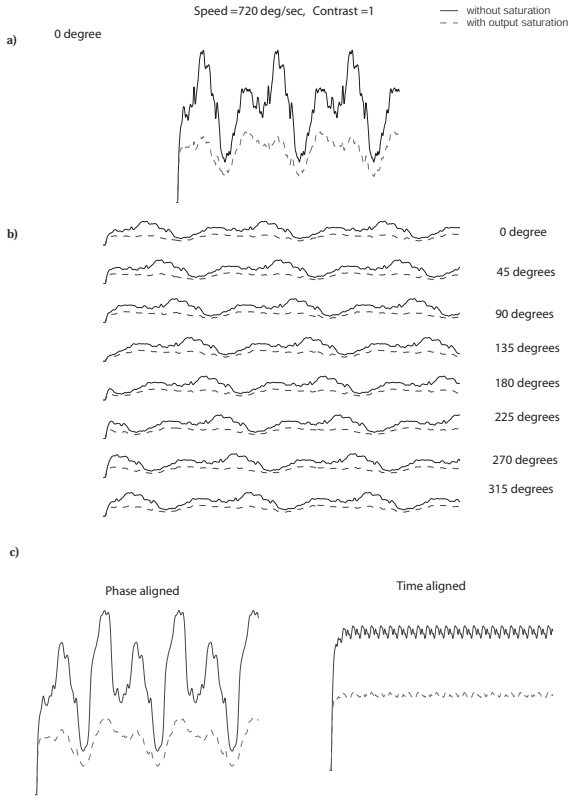


Figure 6. This figure shows the simulation results obtained by running the model with and without implementing output saturation, at 720 degrees per sec at a high contrast of 1 using the same image, at 8 different initial phases, each 45 degrees apart, as done in the physiological experiment shown in Figure 3. Part (a) of the graph shows the response with and without saturation at phase zero. Part (b) shows the response with and without saturation, to each of the 8 configurations. Part (c) shows the response with and without saturation, averaged in two ways, time aligned and phase aligned.[17] Note that pattern noise is more significant at high contrasts and high speeds. Comparison of the model with saturation and without saturation shows that saturation implemented at the out put affects the pattern noise at high contrast by reducing the magnitude of the response and changing the shape of the pattern noise as can be seen from the phase aligned response

We have also tested the effect of saturation at more than one points in the model, on pattern noise. Figure 11 shows the phase aligned simulation results obtained by running the model at 180 degrees per sec at contrast 1 using the same image, at 8 different initial phases, each 45 degrees apart. In the first case, saturation is implemented only at the output stage that is after the outputs of the EMDs are averaged. In the second case, saturation is implemented at the correlator arms before the multiplication stage along with output saturation. And in the third case, saturation is also present at the input, after spatial averaging, along with saturation at the arms and output saturation. It is seen that the shape of the pattern noise changes when saturation is implemented at more than one points with more bumps seen when more saturation is added. This indicates clearly that compressive non-linearity present in the insect visual system affects the pattern noise. It is also clear that the position of saturation in the visual system of insect also has an influence on pattern noise.

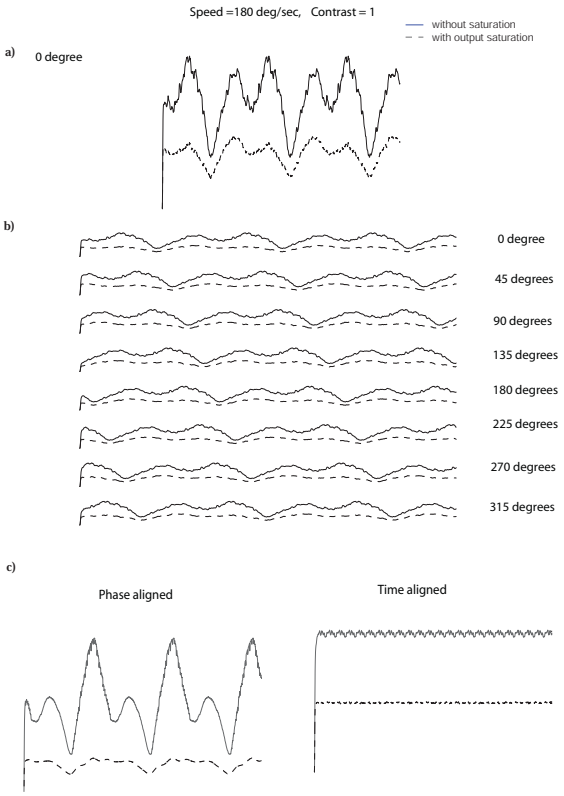


Figure 7. This figure shows the simulation results obtained by running the model with and without implementing output saturation, at 180 degrees per sec at a high contrast of 1, using the same image, at 8 different initial phases, each 45 degrees apart, as done in the physiological experiment shown in Figure 3. Part (a) of the graph shows the response with and without saturation at phase zero. Part (b) shows the response with and without saturation, to each of the 8 configurations. Part (c) shows the response with and without saturation, averaged in two ways, time aligned and phase aligned.[17] Note that pattern noise is more significant at high contrasts and high speeds. Comparison of the model with saturation and without saturation shows that saturation implemented at the output affects the pattern noise at high contrast by reducing the magnitude of the response and changing the shape of the pattern noise as can be seen from the phase aligned response

4. EFFECT OF SATURATION ON CONTRAST DEPENDANCE

Studies carried out by Dror reveal that similarities between natural image power spectra lead to predictable peak response velocities and to similarities in the shapes of the velocity response curves for different natural images. The primary difference between the curves, their overall amplitude, results from contrast differences between images. In order to use mean correlator response as a reliable indicator of velocity, the visual system needs to compensate for these contrast variations.[18, 19] One possibility is contrast saturation early in the motion detection pathway, which eliminates significant differences in contrast[18] and alternatively some form of adaptation (contrast adaptation) in the visual system, may work to remove contrast difference between the images.[20, 21]

Contrast saturation has been found to affect the dependance of the correlator response to contrast.[18] In order to test the effect of saturation on the contrast dependance of the correlator response, we have tested the model by implementing saturation at different points in the model. First saturation is implemented only at the input stage after spatial filtering and the response of one row of EMDs at three different contrast (1, 0.5, 0.1) is shown in Figure 12. Implementing saturation only at the input is found to decrease the dependance of

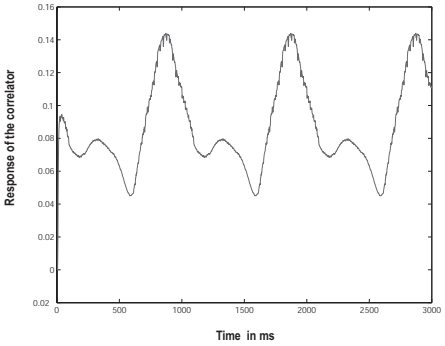
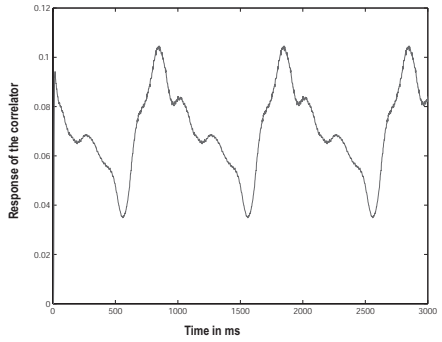


Figure 8. This figure shows the phase aligned simulation results obtained by running the model at 180 degrees per sec using the same image, at 8 different initial phases, each 45 degrees apart. In the phase aligned method, we align each phase delayed response by shifting each response along the x-axis with the data obtained for phase zero and then we average it. The pattern noise present is clearly seen. In this case we have implemented saturation at the correlator input after the spatial filtering stage.



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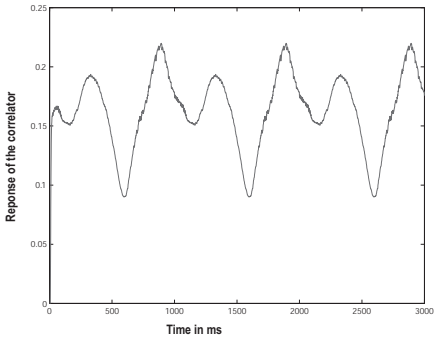
the correlator response on contrast.

Saturation is then implemented only at the correlator arms and the response of one row of EMDs at three different contrast (1, 0.5, 0.1) is shown in Figure 13. It is seen that the addition of compressive non-linearity only at the arms has a remarkable effect on reducing the contrast variations. Saturation implemented at the correlator arms causes more squashing of the response there by decreasing the dependance of the response to contrast further.

And finally saturation is implemented only at the output of the correlators and the response of one row of EMDs at three different contrast (1, 0.5, 0.1) is shown in Figure 14. It is seen that the addition of compressive non-linearity at the output alone has less affect on reducing the contrast variation when compared to the implementation of saturation at the correlator arms. So though saturation at the output reduces the dependance of the response to contrast it has less affect than saturation implemented only at the arms. This could be because this saturation is implemented globally on the mean correlator response where as the



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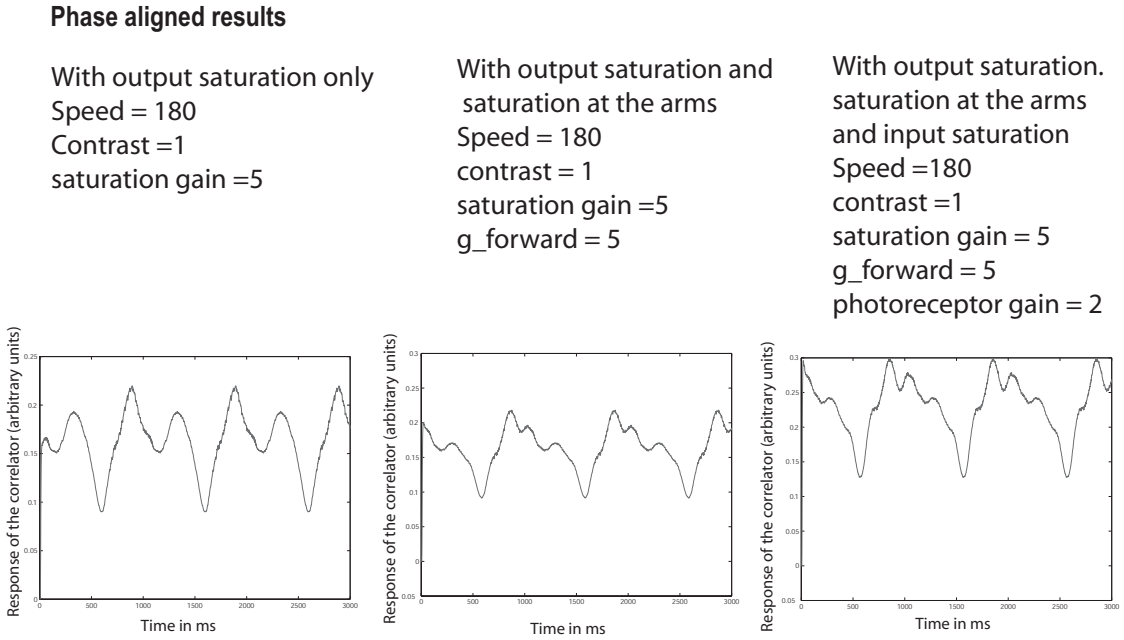

Figure 11. This figure shows the phase aligned simulation results obtained by running the model at 180 degrees per sec at contrast 1 using the same image, at 8 different initial phases, each 45 degrees apart. In the first case, saturation is implemented only at the output stage that is after the outputs of the EMDs are averaged. In the second case, saturation is implemented at the correlator arms before the multiplication stage along with output saturation. And in the third case, saturation is also present at the input, after spatial averaging, along with saturation at the arms and output saturation. It is seen that the shape of the pattern noise changes when saturation is implemented at more than one points with more bumps seen when more saturation is added. It is also clear that the position of saturation in the visual system of insect also has an influence on pattern noise.

saturation implemented at the input and the at the arms is implemented locally on individual local motion detectors.

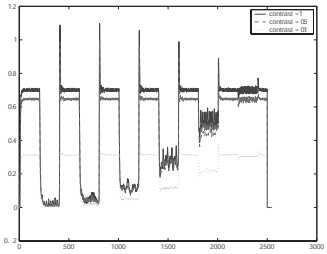

Figure 12. This figure compares the simulated mean response of one row of EMDs of an elaborated model at three different contrasts (1, 0.5, 0.1) with saturation implemented only at the input It is seen that the addition of compressive non-linearity squashes the response of the correlator, thereby reducing the variation of the response to contrast.

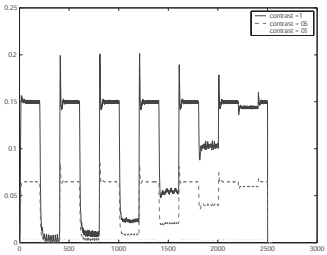

Figure 13. This figure compares the simulated mean response of one row of EMDs of an elaborated model at three different contrasts (1, 0.5, 0.1) with saturation implemented only at the correlator arms. It is seen that the addition of compressive non-linearity only at the arms has a remarkable effect on reducing the contrast variations. Saturation implemented at the correlator arms causes more squashing of the response there by decreasing the dependance of the response to contrast further.

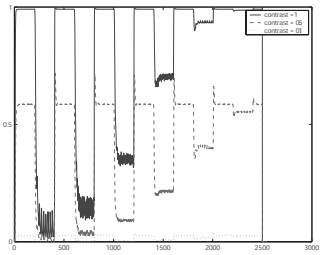

Figure 14. This figure compares the simulated mean response of one row of EMDs of an elaborated model at three different contrasts (1, 0.5, 0.1) with saturation implemented only at the output on the mean EMD response. It is seen that the addition of compressive non-linearity at the output alone has less affect on reducing the contrast variation when compared to the implementation of saturation at the correlator arms. So though saturation at the output reduces the dependance of the response to contrast it has less affect than saturation implemented only at the arms.

4.1. Saturation at more than one points in the model

Here saturation is implemented at more than one points. In the first case, saturation is implemented only at the output of the correlators and the response of one row of EMDs at three different contrast (1, 0.5, 0.1) is shown in Figure 15. In the second case, saturation is implemented at the output as well as the correlator arms and the response of one row of EMDs at three different contrast (1, 0.5, 0.1) is shown and finally saturation is implemented at the output, at the correlator arms and the photoreceptor output and the the response of one row of EMDs at three different contrast (1, 0.5, 0.1) is given. It is seen that the when the compressive non-linearity is added only at the output, the variation of the response is huge with the lowest contrast giving very low response and the highest contrast giving a very high response. But addition of saturation at the

arms decreases the variation of the response to contrast and the further addition of saturation at the input further reduces the effect of contrast on the correlator response suggesting saturation could have a key role in reducing the contrast dependance in fly motion pathway thereby helping them to signal velocity accurately.

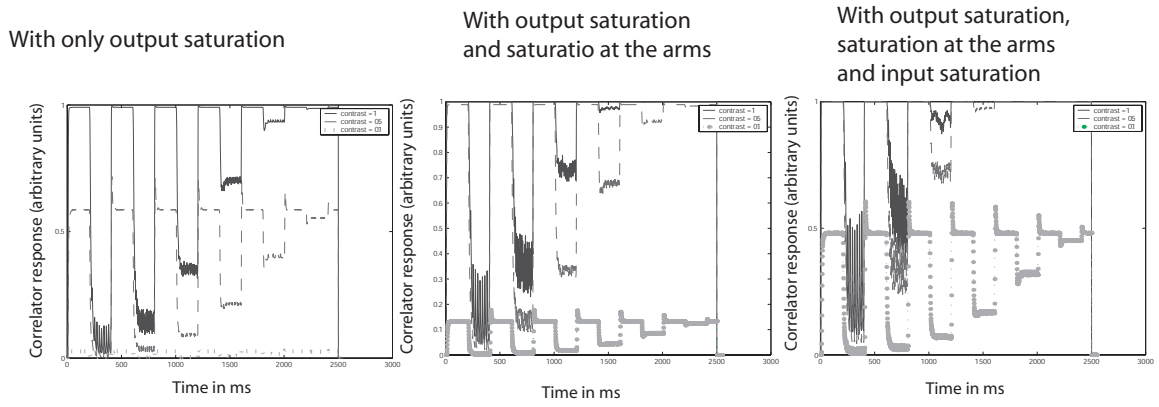

Figure 15. This figure compares the simulated mean response of one row of EMDs of an elaborated model at three different contrasts (1, 0.5, 0.1) with saturation implemented in the first case, only at the output on the mean EMD response. In the second case, satuation is implemented at the output and at the correlator arms and in the third case, saturation is implemented at the output, at the correlator arms and also at the input. It is seen that the addition of compressive non-linearity squashes the response of the correlator. It is seen that the when the compressive non-linearity is added only at the output, the variation of the response is huge with the lowest contrast giving very low response and the highest contrast giving a very high response. But addition of saturation at the arms decreases the variation of the response to contrast and the further addition of saturation at the input further reduces the effect of contrast on the correlator response suggesting saturation could have a key role in reducing the contrast dependance in fly motion pathway thereby helping them to signal velocity accuartely.

5. CONCLUSION

In this paper, we have conducted a study on the effect of saturation on the contrast dependance and on the pattern dependant noise. We have also tried implementing saturation at different points where it can be found in the fly visual system and we have studied its contribution individually and combined together on the response of the EMD array model. We have compared the physiological results with modelling results, and it is seen that our model is able to mimic most of the properties of the physiological data in most of the cases. More experiments are being done in our lab to understand the exact location and contribution of saturation to the fly visual system. But from our preliminary results, here it is clear that saturation could have a key role in decreasing the pattern noise and contrast dependance of the correlator response thereby enabling the fly visual system to signal velocity accurately.

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